WITHIN-NEST BEHAVIOUR IN A EUSOCIAL AUSTRALIAN ALLODAPINE BEE *EXONEURA (EXONEURELLA) TRIDENTATA* HOUSTON (APIDAE: XYLOCOPINAE)

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Summary

STEEN, Z. & SCHWARZ, M. P. (1998) Within-nest behaviour in a eusocial Australian allodapine bee *Exoneura (Exoneurella) tridentata* Houston (Apidae: Xylocopinae). *Trans. R. Soc. S. Aust.* **122**(2), 55-63, 29 May, 1998.

Understanding the processes involved in the evolution of social behaviour has become one of the most challenging areas of modern biology. Since bees and wasps exhibit a variety of social organisations they are particularly useful for addressing social evolutionary questions. Allodapine bees are especially useful for examining social evolution, since species display varying forms of social organisation from solitary to eusocial. This study examines within-nest behaviour of *Exoneura (Exoneurella) tridentata*, a native Australian allodapine bee. This species has the largest known colony sizes of any allodapine bee and exhibits striking size variation among female nestmates suggesting that sociality may be regarded as highly eusocial. Here we assemble a behavioural catalogue for this species and show that although many behaviours are similar to those recorded for other allodapines, this species differs by the marked presence of overt aggression displayed in the form of biting. Overtly agonistic behaviours have not been recorded for other Australian allodapines and have been recorded only rarely in other allodapine fauna. *Exoneura tridentata* appears to differ from other highly eusocial species where there is usually little or no aggression but instead "gentle despotism".

KEY WORDS: *Exoneura tridentata*, social behaviour, allodapine bees, aggression.

Introduction

The allodapine bees provide opportunities for comparative approaches to the evolution of social behaviour because of the wide range of social organisation within and between species and genera. One small and endemic Australian subgenus *Exoneurella*, contains fours species that range from the predominantly solitary *Exoneura lawsoni* Rayment (Michener 1965) to the eusocial *E. tridentata* (Houston 1977; Hurst & Schwarz 1996).

In most comparative studies of insect social evolution there is an implicit assumption that small colony size is associated with flexible and behaviourally mediated reproductive skew. The maintenance of dominance hierarchies via physical agonism is considered a primitive trait (Wilson 1971). Correspondingly, large colony sizes with strong reproductive skew and non-agonistically maintained hierarchies are usually regarded as more derived traits. Wilson (1971) suggested that less sophisticated forms of social organisation would involve physical mechanisms of control such as aggression within a colony, but that this is replaced by "gentle despotism" in more advanced forms of sociality. It is also generally assumed that a high level of behavioural specialisation is a more derived trait and that this can lead to higher levels of colony efficiency (Jeanne 1986). However, the idea that different forms of social organisation can be arranged in a sequence of 'primitive' to 'advanced' has been questioned (Kukuk 1995) but few studies have explicitly investigated whether 'primitive' or 'advanced' forms of sociality within taxa correspond to basal or distal positions within phylogenetic trees.

Exoneura tridentata is an Australian allodapine bee that lives in semi-arid environments. This species has the largest known colony sizes of any allodapine bee and exhibits morphological differentiation between putative castes (Houston 1977, Hurst & Schwarz 1996). Much of the information about social organisation has been inferred from dissection of nest occupants and brief observations of females outside of their nests (Houston 1977; Hurst unpub.). It is suspected that this species exhibits caste differentiation, where large females (termed 'Majors') are queen-like and smaller females ('Minors') act as workers within the colonies (Houston 1977; Hurst 1996). However, within-nest behavioural studies have not been carried out to assess whether these two morphs really are behaviourally distinct. Colony size and the association between morphology and reproductive status suggest that this species more closely approaches the highly eusocial form of organisation characteristic of apine, meliponine and highly eusocial halictine bees, than any other allodapine bee.

This study investigates within-nest behaviour in observation colonies of *E. tridentata*. A repertoire of behaviours is presented here in the form of a behavioural catalogue and compared with other behavioural studies of allodapines. These data will also be used for specific analysis of behavioural specialisation, which will appear in a future series of

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publications. In addition, the idea that morphological caste differentiation and large colony size are associated with low levels of agonism in colony integration is discussed in relation to the social organisation of *E. tridentata*.

Materials and Methods

Study sites

Exoneura tridentata nests were collected from Lake Gilles Conservation Park (136 48' E, 32 54' S) located in the north east of Eyre Peninsula, South Australia. In this area, *E. tridentata* nests were principally in disused beetle burrows excavated in *Acacia pycnocarpa* Benth. (Western Myall) and *Halgetryon oleiofolium* (Desf.). (Bullock Bush). Dead branches of both tree species were examined for nest entrances i.e. the exit holes made by the original beetle occupants. Intact colonies were collected during February 1995. Field collection of nests took place when temperatures were cool (12 C-20 C), to ensure that all occupants were present. Once an entrance hole was located, the branch was removed, entrances were blocked with tissue paper, the branch was placed in a waterproof bag and stored in an insulated container with ice for transport to Flinders University.

At Flinders University the nests were stored in a constant temperature room at approximately 10 C for processing. Nests were opened using a knife and all nest occupants, including brood and nest contents such as pollen, were transferred to a Petri dish. Adults were individually marked using Humbrol™ and Testors™ enamel paints applied to the thorax and metasoma. Bee colonies were then transferred to artificial observation nests.

Artificial nests were similar in design to those described by Schwarz & Overholt (1993) but were made of pine wood instead of balsa. Each nest consisted of a rectangular piece of untreated pine wood 210 x 20 x 15 mm. A groove was gouged into one longitudinal face (5 mm diam x 200 mm length). The groove was smoothed out with a metal rod to remove any splinters of wood. A piece of glass, 210 x 20 mm, was placed flush against the groove and secured at both ends with insulation tape. A black cardboard cover was placed over the glass to exclude light between observation periods.

Observation nests were set up on subhorizontal trays in a shade house at Flinders University. One end of the shade house was open so that bees could forage freely outside. Nest entrances faced the open end of the shade house. A maximum of four nests was placed on each tray with approximately 15 cm between each nest. Observation nests were first placed in the shade house at dusk 5-6 days after collection and opening. This ensured that the bees had approximately 12 hours in the artificial nest to allow their odours to permeate the nest before it was possible for them to leave (the next morning). Sticks were haphazardly placed near nests to act as visual cues for returning bees.

Behavioural observations

Once observation nests were set up bees were allowed to adjust to their new environment for one week before observations began. Data collection involved 'scan' and 'focal' sampling techniques (Altman 1974). Scan sampling involved recording the position of each individual in the observation nest, using a 5 mm scale along the glass and was conducted immediately before and after focal sampling. This was done to determine whether certain bees were spending more time than others in certain areas of the nest, for example, near the entrance or near the brood. Focal sampling involved 2 min observations of each bee in a nest. Nests and individuals were randomly selected each day for order of observations. A headband magnifier (x 5.2 magnification) was used to observe the behaviour of individuals. All behaviours performed in a 2 min period for each individual were recorded into a voice operated recorder. Observations were transcribed on to data sheets at a later date. These behavioural data were used to construct the behavioural catalogue and later to examine behavioural specialisation.

Behavioural observations took place in the afternoon, (1300-1700 h), when temperatures were ≥ 20 C and bees were active. In total, 10 nests were observed with up to four nests being observed in any one session. Table 1 provides information about which nests were observed, when they were observed and how many minutes of observation each bee per nest received. In addition, the numbers of bees that were present for the initial and final observation periods are given.

Results

Field-collected nests

The contents of nests collected in February 1995 are summarised in Table 2. During these sampling periods, colonies used for behavioural observations were rearing brood. In early February colonies contained brood of all developmental stages, i.e. eggs, larvae, prepupae and pupae. By late February female bees in the colonies had almost ceased egg laying and brood mostly comprised larvae, prepupae and pupae. There was a great deal of variation in the number of adult females present in a nest, ranging from 1-18 (Fig. 1).

TABLE 1. *Details for nests of* Exoneura tridentata *observed in this study.*

Nest	First observations	Last observations	Total number of observation periods per nest	Total minutes of observation per bee per nest	Initial no. of Individuals	Final no. of Individuals
1	7 Mar.	14 Apr.	15	30	8	5[a]
6	7 Mar.	14 Apr.	15	30	9	5[a]
9	7 Mar.	14 Apr.	15	30	9	12[b]
12	7 Mar.	14 Apr.	15	30	13	15[b]
3	5 Apr.	4 May	19	38	5	5
4	5 Apr	4 May	19	38	4	5[b]
20	5 Apr	4 May	19	38	4	5[c]
30	26 Apr.	16 May	20	40	6	5[a]
43	26 Apr.	16 May	20	40	3	4[b]
56	29 Apr.	16 May	20	40	4	4

Decreases in the number of indivduals were probably due to death whilst foraging or dispersal to other nests[a]. Increases were due to the addition of newly eclosed bees[b], or intruders which swapped nests[c].

TABLE 2. *Summary of nest contents for colonies of* Exoneura tridentata *collected in February 1995 from Lake Gilles, South Australia.*

Nest contents	Mean value (±S.E.) for early February (N=24)	Mean value (±S.E.) for late February (N=13)
Eggs	1.21 (0.57)	0.08 (0.08)
Larvae	1.75 (0.63)	0.62 (0.27)
Prepupae	0.67 (0.28)	0.31 (0.13)
Pupae	2.42 (0.72)	2.23 (0.70)
Majors	1.17 (0.16)	1.23 (0.34)
Minors	4.17 (0.83)	4.38 (1.30)
Males	0.33 (0.13)	0.38 (0.21)

Behavioural repertoire

In the following section behaviours observed during the study are presented as a behavioural catalogue. Observed behaviours are classified into four functional groups (often inter-connected or overlapping): (i) self maintenance behaviours, (ii) nest maintenance behaviours, (iii) inter-adult behaviours, and (iv) adult-brood interactions.

SELF-MAINTENANCE BEHAVIOURS

INACTIVE

Bees were recorded as being "inactive" when no other behaviour was being performed. Inactivity often occurred within a behavioural sequence. For example, a bee could stop grooming, be inactive for some time, and then travel forward in the nest. Bees could either be standing 'upright' or they could be lying 'upside down' on the floor of the nest. Maeta *et al.* (1992) included slight movements in their description of a similar behaviour, "Resting". However, in this study bees were only recorded as

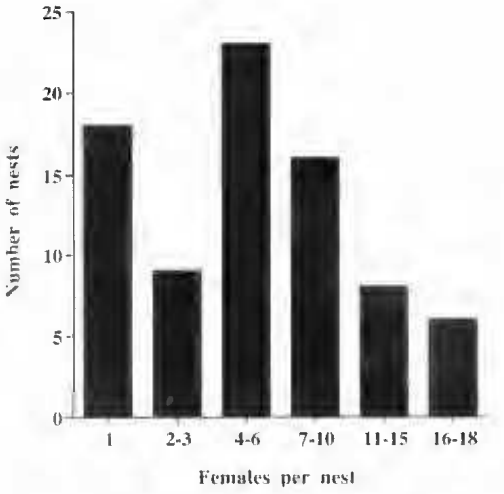

Fig. 1. Histogram of colony sizes (number of females per nest) of *Exoneura tridentata* collected from Lake Gilles South Australia, February 1995.

inactive when they were motionless. *Exoneura tridentata* spent a large amount of time inactive. Since inactivity can occur within and between behavioural sequences it is difficult to show numerically the amount of time spent inactive because of the way the data were collected. Generally, though, the bees were more active when temperatures were >20° C and/or when a forager returned.

SELF GROOMING

"Grooming" was observed frequently, and included any activity where the body surface was cleaned. Sequences for cleaning different areas of the body were similar to those reported for *Braunsapis hewitti* Cameron and *Ceratina* spp., (Maeta *et al.* 1992). The most common sequences were: (a) head cleaned by initially wiping a foreleg with the proboscis then foreleg used to wipe the length of the antennae, beginning at the base; foreleg again wiped with the proboscis, followed by the wiping of the head with the forelegs, (b) the metasoma was cleaned by using the tibial spurs on the hindlegs to scrape off dust/pollen, (c) the thorax was cleaned with the mid legs (the metasoma and the thorax were often groomed at the same time with the different legs), (d) the wing surfaces were groomed by dragging the wings under the metasoma with the hind legs, wiping them between the metasoma and hind legs, and then flicking them back into position. Grooming did not occur as one long uninterrupted sequence as has been observed for *B. hewitti* (Maeta *et al.* 1992). Grooming could be brief or last for the whole 2 min observation period.

SLIGHT BODY MOVEMENTS

This was intermittent behaviour, which was often observed during long bouts of inactivity, and behaviour comprised slight movements of head, body or legs, which did not involve any other type of behaviour.

TRAVELLING

"Travelling" involved moving forwards or backwards up or down the nest for 1-20 cm. Bees that were travelling were usually very active but the travelling speed varied. Travelling forward often resulted in a bee coming into contact with others and was usually followed by "passing" (see below).

TURNING

"Turning" was used to describe a change of direction in the nest. Turning involved curling the body and somersaulting, resulting in the bee facing the opposite direction. Both Majors and Minors appeared to turn with equal ease. This behaviour occurred anywhere in the nest, unlike that in *Ceratina* spp. which have a turning burrow enlargement near the nest entrance (Maeta *et al.* 1992). Turning often occurred as part of a sequence of behaviours during interactions between individuals, i.e. it could occur during sequences which involved "nudging", "passing" or "avoidance" (see below). If a bee approached but avoided another bee, it might either "travel" up to the bee, and then back away or it might "turn" and "travel" in the opposite direction.

NECTAR DEHYDRATION

Individuals were observed flexing and bending the proboscis and, although droplets of nectar could not be seen with at the magnifications used, it was assumed that they were dehydrating nectar as has been observed in other allodapines after feeding (Michener 1972; Maeta *et al.* 1992). Some bees slowly fully extended and retracted the whole proboscis without bending it. The proboscis was extended and held out for about 20 sec then retracted before being extended again. Some individuals spent the whole two min observation period performing this behaviour.

NEST ABSENTEEISM

When individuals were regularly absent from the nest it was assumed that they were foraging. However, if they were absent for more than 5 observation sessions in a row, it was assumed that they were either dead or had dispersed. Absenteeism (or foraging activity) was only observed when temperatures were ≥ 25° C. Foragers were identified when they were seen returning to the nest. Upon returning, foragers usually worked their way down the nest passing and interacting with other individuals, often having "buccal contact" with other individuals, presumably providing them with nectar (see inter-adult behaviours). Often such a bee would then leave the nest again and return later. Foragers were not observed feeding larvae.

NEST MAINTENANCE BEHAVIOURS

GUARDING

A bee was recorded as "guarding" when it occupied the position closest to the nest entrance with its body oriented so that its head was facing away from the entrance. Such a position allows the metasoma to block the nest entrance from intruders, as recorded for other allodapine bees *B. hewitti* (Maeta *et al.* 1992), *B. mixta* (Batra *et al.* 1993) and *E. bicolor* (Melha & Schwarz 1993). During guarding the bee was inactive either on its back or standing upright. If a bee was closest to and facing the nest entrance, it was not recorded as guarding, since bees in this position would often be in the process of leaving

the nest. Minors were often seen guarding and in some nests, Majors, particularly egg-layers, were not seen to guard at all.

Guarding did not always occur near the nest entrance. In some nests the "guard" was stationed 1/4-1/3 of the way down the nest but was the bee closest to the nest entrance. These guards were sometimes seen to 'patrol' the nest from that section up to the entrance. This involved the bee rapidly "travelling" forward, whilst rapidly antennating ("inspecting") the nest lumen before returning to the guard position. In some nests it also appeared that two individuals would guard alternately or one in front of the other. Although there were times when more than one individual was seen in the guard position, there were individuals who never "guarded". During the study, no other invertebrates were observed entering the nests. Since there was no interference from other invertebrate predators in the captive situation, guarding in this study may not reflect natural behaviour of this species.

INSPECTING

This behaviour involved a bee alternately antennating objects, for example the nest wall or brood. Eggs were frequently antennated in this way. Sometimes bees travelled up and down the nest inspecting the lumen wall. During this behaviour bees moved their heads slightly and rapidly moved antennae.

MOVING DEBRIS

Debris in the nest was moved by passing it under the body with the forelegs to the hind legs then pushing backwards with the hind legs or metasoma. This behaviour was rare (approx. 0.3% of the observation time), since the nests were in hard, fine-grained wood which required little maintenance. Debris observed in the nest included exuviae and, occasionally, dead individuals. "Moving debris" was not usually observed unless temperatures were ≥ 25°C.

INTER-ADULT BEHAVIOURS

AVOIDANCE

"Avoidance", a combination of other behaviours, involved one individual travelling towards another individual and "antennating" either the metasoma or face of that individual and then suddenly backing away or turning and travelling in the opposite direction.

ANTENNAL CONTACT

"Antennal contact" accompanied most inter-adult behaviours. When an individual came in to contact with another individual it either "antennated" the other's metasoma or face. If individuals were face-to-face the two individuals tapped each other's antennae.

PASSING

"Passing" is the exchange of positions by nest mates. Passing occurred when individuals were either facing each other or the "passer" was facing the metasoma of the individual she intended to pass. In each case, individuals oriented themselves venter-to-venter, essentially walking over each other. A pass was either simple or complex. "Simple passing" involved the smooth exchange of positions, with individuals usually flattening their bodies against the nest wall. "Complex passing" involved one individual biting at another individual's body parts, and/or struggling and grasping each other with the legs. Either one or both individuals would bite. Sometimes one individual would bite the other on the ventral side between the metasoma and the thorax, near the articulation between the trochanter and the thorax. Passing sometimes involved brief "buccal contact" between the two individuals, although it was often difficult to determine clearly whether buccal contact had actually occurred. It was not always easy to distinguish between the passer and the "passed", except when one was initially stationary and another was travelling.

BUCCAL CONTACT

Individuals were often observed to touch each other's open mandibles with their own open mandibles; this was termed "buccal contact". When individuals were involved in such interactions, one individual was standing upright and the other was positioned upside down. Individuals also engaged in brief buccal contact during passing. During approximately 5% of buccal contact interactions, nectar flow between the mouth parts of individuals was observed and individuals were observed placing their proboscis between the mandibles of another individual. Proffering of globules of nectar (Melna & Schwarz 1993), was not observed in *E. tridentata*.

NUDGING

"Nudging" involved one individual using its face to nudge or butt the metasoma or face of another individual. The bee that "nudged" was usually upright. Nudging usually resulted in one of the following:

a) The nudged individual turned and the nudger retreated, which sometimes involved the nudged bee opening its mandibles.

b) If nudged from behind, the bee being nudged would sometimes position its antennae laterally (out to the side), then if nudged again it might open its mandibles. This eventually resulted in the bee

turning, investigating the "nudger", and then simple or complex passing and/or buccal contact.
c) The nudged or the nudger passing and "biting" each other.

MANDIBULATING

Mandibulating, i.e. the opening and closing of the mandibles not associated with eating, appeared to occur before biting encounters. In some cases it appeared that mandibulating was a signal that one individual was rejecting an approach from another individual. For example 'A' approached 'B', 'A' nudged 'B', 'B' then opened mandibles, 'A' then retreated. "Biting" encounters sometimes followed. Similarly, if an individual was nudged from behind it sometimes opened its mandibles and/or turned and faced the nudger often opening the mandibles again. In addition, flattening of the antennae laterally often occurred during mandibulating. This sometimes occurred when individuals came face to face or if one was nudged from behind.

BITING

In this study aggressive encounters were observed for *E. tridentata*. These involved biting of mandibles, antennae, neck, legs, the ventral side of the thorax, around the coxae and metasoma. Often when one individual tried to escape from such an encounter the other bee would pull it back using its forelegs. "Biting" encounters were often complex. For example, 'A' used its face to nudge 'B's face. Then one or both bees opened the mandibles and a complicated pass followed. Whilst the bees were venter to venter and struggling (holding each other with legs) one would bite the other on the ventral side of the thorax. After a struggle, the bitten bee was often observed on its back while the biter held the other bee's antennae in its mandibles, in a "Tug of-war" encounter. This tug-of-war could last for 10-20 sec. Following a tug-of-war encounter the individual which had initiated the pass (the biter) sometimes attempted to pass again and often a simple pass would follow.

ADULT-BROOD INTERACTIONS

EXAMINATION OF BROOD

Examination of brood was accomplished with the antennae, and, to a lesser extent, the mouth parts (opening and closing mandibles on the brood). Individuals tapped pupae, larvae or eggs, with each antenna.

NUDGING BROOD

Brood were sometimes nudged before they were moved. This behaviour did not result, however, in the brood appreciably changing position.

MOVING BROOD

Older brood (late instar larvae, prepupae and pupae) were usually moved in a way similar to the way debris was moved in the nest. In *E. tridentata*, similar to *E. bicolor* (P. S. Hurst pers. comm. 1995), the bee initially held the brood with the fore tarsi then passed them under the body and pushed them backwards using the hind legs. Repositioning of brood occurred often within the nests of *E. tridentata*. Sometimes a bee would move each pupa until it reached the end of the nest, then it would move them all back again; seconds later another individual sometimes did the same thing. Some Minors which consistently stayed near the brood were often observed performing this behaviour. In addition, bees sometimes simply handled the pupae with the fore legs but did not actually reposition them.

GROOMING BROOD

Bees occasionally extended the proboscis to the brood or bit gently at the brood with their mandibles; such behaviour was categorised as "grooming brood". This behaviour was rarely observed. Grooming may have occurred during moving or with handling but it was difficult to observe the finer movements of such behaviour because of the speed of movement of the proboscis and the limited magnification.

OVIPOSITION

When "Ovipositing", the female oriented herself so that the head pointed towards the nest entrance. During egg laying bees were observed in one of three positions: ventral surface facing upwards, dorsal surface facing upwards and lateral surface facing upwards. Prior to and during "Oviposition" the sting was extended. Once an egg had been deposited on the floor of the nest, the bee retracted the sting. Approximately 1-6 min passed before the female turned around and inspected the egg with the antennae.

Oviposition occurred close to the nest end (0.5 mm) and was observed for 4 Majors and 1 Minor (5 separate colonies). Individuals took approximately 5-6 min to discharge an egg. However, one Major took 38 min to lay an egg.

Discussion

Behaviour has previously been studied in detail for *B. brevili* (Macta *et al.* 1992), *B. nivata*, *B. kallaga* (Batra *et al.* 1993), *Allodape exclusa* (Strand) (Mason 1988) and *E. bicolor* (Mehta & Schwarz 1993). *Exoneura tridentata* generally spend a large amount of time inactive, similar to other bees (Macta *et al.* 1992; Batra *et al.* 1993). Activity tended to be greater on days when the temperatures were above

25 °C. Similarly, when the temperature was warmer bees tended to forage more and, especially after return of a forager to the nest, general activity appeared to increase.

Exoneura tridentata was not observed to exhibit the types of nest maintenance behaviours found in other allodapines, probably due to the hard nature of the nest substrate. Most allodapines excavate their own nests in pithy substrate material, whereas *E. tridentata* do not. Although observation nests provided no opportunity for nest walls to decay during the course of the study, natural nests are also unlikely to require repairs to the nest wall or entrance, since they also occur in fine grained wood. This contrasts with *E. bicolor* which performs various nest maintenance activities such as clearing and lamping (removing loose material from the nest wall and shaping nest lumen), extending the nest lumen (excavating rear of the burrow), collar construction (lamping wood into a collar near nest entrance) and removing debris (wood strands). *Exoneura tridentata* may exhibit nest maintenance activities to a greater degree when new nests are founded and there is a need to remove frass left behind by beetle larvae.

This study is the first to describe egg laying in an *Exoneura* species. Egg laying was only observed during the day, although it may also have occurred at night (observations were only made during the day). Egg laying was similar to that described for *B. mixta* (Batra *et al.* 1993) and *B. hewitti* (Maeta *et al.* 1992). However, two of the three *E. tridentata* majors that were observed ovipositing were rarely or never seen guarding. The third major was seen to guard but she was usually 5 cm from the base of the nest and not near the entrance. This differs from *B. hewitti* (Maeta *et al.* 1992) and *E. bicolor* (Hogendoorn & Schwarz 1998; Bull *et al.* in press) where reproductive dominants are guards. Egg laying in this species appears to be a very slow process compared with other bees (58 sec. *B. hewitti*) (Maeta *et al.* 1992), in terms of both the time taken to deposit an egg and the frequency of egg laying. One female, in particular, spent 38 min depositing an egg which may have been related to the fact that the temperature was low that day (< 20 °C), and bees were generally less active at lower temperatures. However, these observations did not cover the period of maximal egg production and should be treated with caution.

Aggressive behaviour has not been reported for other allodapine bees except rarely between *B. mixta* and its social parasite *B. kalitaga* (Batra *et al.* 1993) and infrequently for *A. exoloma* and *B. fiorata* (Mason 1988). The agonistic behaviour described for these species mainly consisted of nudging, biting of legs and bodies and blocking passage, but also included stinging (Batra *et al.* 1993; Mason 1988). Agonistic behaviour between a host and its parasite is not uncommon and often results in either host or parasite being removed from the nest (Batra *et al.* 1993). Aggressive interactions are also found in social species of the bee tribes Halictini and Xylocopini (Breed *et al.* 1978; Michener 1990). However, *E. tridentata* was often observed to engage in aggressive encounters which involved a great deal of biting and struggling, with some encounters becoming quite savage. Such encounters were often preceded by nudging and followed by passing. The mandibulating that occurred sometimes, either prior to or in response to nudging and biting, might also be aggressive in nature. Cane & Michener (1983) found that some *Exoneura* spp. produce irritants which elicit vigorous grooming responses in predatory ants. Batra *et al.* (1993) described mandibulating during aggression between *B. mixta* and its social parasite *B. kalitaga* and suggested that mandibular secretions were involved. It may therefore be suggested that when *E. tridentata* mandibulate at each other, they also release chemical secretions which may be agonistic or relay information about dominance status.

The agonistic behaviours observed in *E. tridentata* suggest that dominance hierarchies may be present within colonies. It appears that some individuals engage in certain types of behaviour which could be interpreted as assertion of dominance. Bees that are often nudged or bitten and those that exhibit avoidance behaviour may have more subordinate roles in the nest. Differences in the way individuals respond to other individuals in terms of these behaviours may be related to dominance (i.e. when some individuals are nudged they engage in a simple pass, whereas when other individuals are nudged and/or bitten they engage in a complicated pass). Brothers & Michener (1974) found that 'queens' of *Lasioglossum zephyrum* were the maximal nudgers in the colony. They suggested that nudging behaviour indicates dominance similar to that observed in other primitively eusocial wasps and bees. Brothers & Michener (1974) experimentally showed, for *L. zephyrum*, that nudging by the queen plays a role in the division of labour among the workers by inhibiting ovarian development.

During this study guarding behaviour was not the same as that observed in field studies of *E. tridentata*, i.e. with the abdomen curled and used to block the entrance from predators such as ants (Hurst unpub.). This may be related to the fact that there was no predation pressure in the shade house environment, unlike studies on *E. bicolor* conducted in shade houses where ants were a problem (Bull[1];Hurst[2]). However, females that were guarding were always facing the bottom of the nest which suggests that

they were in a position to block the nest if the need arose.

Trophallaxis is altruistic behaviour; foragers engage in energetically costly and risky behaviour to obtain food which they relinquish to others. Trophallaxis is important in the social organisation of many social insects (Wilson 1971). In allodapines there may be differences in the way in which trophallaxis is performed. *Exoneura bicolor* have been observed to engage in solicitation behaviour before trophallaxis occurs (Melna & Schwarz 1993). Solicitation involved individuals rapidly stroking each other's antennae prior to buccal contact. Trophallaxis in *E. bicolor* can also involve one individual proffering a globule of liquid to another (Melna & Schwarz 1993). Proffering of globules was not observed in *E. tridentata* and if solicitation occurred, it was too fast to be identified. However, it is likely that individuals which engaged in "buccal contact" where nectar flow was observed, were frequently engaging in trophallaxis. Trophallaxis allows females to feed without leaving the nest. The presence of trophallaxis in *E. tridentata* therefore allows behavioural specialisation where only some of the females have to forage and other females can perform other duties in the nest.

Exoneura tridentata exhibits a similar repertoire of behaviours to other allodapines (Maeta *et al.* 1992; Batra *et al.* 1993; Melna & Schwarz 1993). Behaviours recorded in this study, including adult-adult interactions and adult-brood interactions, are all similar to those found for other species, suggesting that such behaviours are likely to be ancestral and that development of novel behavioural elements is not necessary for social organisation to evolve from small family groups to large groups with morphological differentiation among colony members.

However, unlike other allodapines, *E. tridentata* exhibits frequent and overt agonistic behaviours among nest mates. Such agonistic behaviour has often been associated with more primitively social species. According to Wilson's (1971) criteria, *E. tridentata* can be classed as highly eusocial because there is female morphological dimorphism associated with reproductive division of labour. Therefore, *E. tridentata* doesn't conform to Wilson's (1971) suggestion that aggression within a colony can be replaced by "gentle despotism" as sociality involves larger group size and requires a greater degree of integration. Most other highly eusocial species display distinct morphs which are directly associated with discrete behavioural castes, involving minimal or no aggression. Considering the presence of aggressive interactions within *E. tridentata* colonies, it would seem that increased colony size and the development of morphological differentiation among colony members need not be accompanied by decreased levels of overt intra-colony aggression.

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